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Host Recognition Kairomones for *Anaphes iole* Girault, an Egg Parasitoid of the Western Tarnished Plant Bug[1]

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Laboratory experiments were conducted to determine if chemicals derived from host adults or eggs influence the host location/recognition behavior of *Anaphes iole* Girault (Hymenoptera: Mymaridae) females. Females often probed with their ovipositor, in or near punctures made by *Lygus hesperus* Knight (Hemiptera:Miridae) females on Gelcarin oviposition packs, in a way that was similar to the probing of protruding host eggs. When the surface Parafilm of the Gelcarin packs that *L. hesperus* females had oviposited was replaced with clean punctured Parafilm, females also responded to the punctures, suggesting that the internal contents of the Gelcarin packs cause the probing behavior. Females probed punctures on a piece of Parafilm covering the abdominal contents of host females and males, but they did not respond to punctures in Parafilm covering distilled water or Rinaldini solution. Females also probed glass cylinders coated with host hemolymph, contents of host females or males, or seminal depository. These results suggest that *A. iole* females use chemicals derived from host eggs or adults in host recognition. Because females responded to mature ovarian eggs embedded in Gelcarin packs, a possible source of this stimulant may be the ovaries of the *L. hesperus* females. Punctured Parafilm removed from Gelcarin packs which host nymphs had probed with their mouthparts stimulated antennation by *A. iole* females, but not ovipositor probing. Punctures on Gelcarin packs that had never been exposed to hosts sometimes stimulated ovipositor probing by female *A. iole*. Because the probing response was not elicited from *A. iole* females by punctured Parafilm covering nothing, distilled water, or liquid from Gelcarin packs, the presence of the gel underneath punctured Parafilm may elicit an ovipositor probing response from *A. iole* females. Host-derived chemicals play an important role with physical properties of host eggs and the substrate in which host eggs are embedded, on host recognition and acceptance by *A. iole* females.

***Key Words: Anaphes iole; Lygus hesperus;* host selection; Kairomone; insect rearing; biological control.**

INTRODUCTION

A variety of physical and/or chemical stimuli from host eggs, products from adult hosts, or from the plants on which the host feeds mediate host location and selection behavior of egg parasitoids (see reviews by Nordlund *et al.*, 1981; Vinson, 1985; Nordlund, 1994; Schmidt, 1994). The host recognition process for parasitoids that attack exposed host eggs on plant surface is influenced by chemicals left on egg chorion by host adults, such as adhesives, and the egg's physical properties, such as shape and size (Strand and Vinson, 1982, 1983; Vinson and Piper, 1986; Nordlund *et al.*, 1987; Bin *et al.*, 1993). Although egg parasitoids may also respond to volatile chemicals released by host-infested plants to locate the host's habitats (Nordlund, 1994), plant chemicals may not be important in the host recognition and acceptance steps.

However, unlike these egg parasitoids, mymarid wasps often attack eggs that are partially or fully embedded in plant tissues (Clancy and Pierce, 1966; Jackson and Graham, 1983; Cronin and Strong, 1990; Conti *et al.*, 1996). Plant-derived stimuli, emanating from wounds made by adult hosts, may be important in host recognition or acceptance by parasitoids that attack host eggs embedded in plant tissues, because the host eggs are not fully exposed. Also, insects that oviposit in plant tissues may do so without adhesives which are known to function in host recognition by parasitoids that attack exposed host eggs (Strand and Vinson, 1982; Nordlund *et al.*, 1987; Bin *et al.*, 1993). The host

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selection mechanism of parasitoids attacking embedded eggs has rarely been studied and remains poorly known (Conti *et al.*, 1996).

Anaphes iole Girault attacks the eggs of *Lygus* spp. (Graham and Jackson, 1982; Graham *et al.*, 1986; Sohati *et al.*, 1992), which are embedded in plant tissues (Clancy and Pierce, 1966; Jackson and Graham, 1983; Huber and Rajakulendran, 1988). Conti *et al.* (1996) demonstrated that the shape and position of the portion of the egg that protrudes from the plant surface are important in host recognition by *A. iole*. Although it has also been suggested that chemicals emanating from hosts or plant wounds may play an important role in host location and recognition (Conti *et al.*, 1996, 1997), the source of chemical cues involved in the host selection behavior of *A. iole* has not yet been identified. In the present study, we conducted laboratory experiments to determine if chemical cues derived from host eggs or host adults are involved in the host recognition or acceptance behavior of *A. iole* females.

MATERIALS AND METHODS

Insects

Lygus hesperus Knight were reared in a manner similar to that described by Debolt and Patana (1985). However, a new artifical diet (Cohen, 2000) was used. To collect eggs, we used Gelcarin (a food-grade gelling agent, FMC, Food Ingredients Division, Rockland, ME) oviposition packs similar to those described by Debolt and Patana (1985). The dry Gelcarin (20 g) was blended with hot distilled water (1 L). The resulting solution was autoclaved for 20 min and then held at 66°C to keep it liquid. A piece of Parafilm (American National Can, Greenwich, CT)(5 × 10 cm) was folded in half and heat-sealed on two sides to form a bag. The Parafilm bag was filled with the warm Gelcarin solution, and the fourth side was heat-sealed to form a pack (5 × 5 cm). When the Gelcarin cooled, it gelled and retained its flat shape. After the Gelcarin cooled, packs were placed on the screened top of a cage containing adults (or nymphs for one experiment) for ca. 24 h to receive the eggs. In some experiments, Gelcarin packs that had not been exposed to *L. hesperus* were used.

A. iole were obtained as cocoons or adults from Biotactics Inc. (Perris, California). Adult parasitoids were held at ca. 25°C under a 16L:8D photoregime. Immediately before an experiment, 1- to 3-day-old females were exposed to host eggs embedded in a Gelcarin pack and allowed to oviposit for 1–2 h. Only females that had been observed to oviposit during this period were used in subsequent experiments because some females never responded to host eggs embedded in the Gelcarin packs.

Effect of Substances in Gelcarin Packs on Host Recognition

On Gelcarin packs on which *L. hesperus* eggs had been laid, *A. iole* females often probed not only host eggs but in or near ovipositor punctures (without eggs) made by host females. Thus, we suspected that females might respond to substances from the host female or host egg: *L. hesperus* females might secrete some chemicals during oviposition into Gelcarin packs, or chemicals of the egg's surface may dissolved in the packs. Thus, we first determined if the wasp's response to punctures was stimulated by materials deposited inside the Gelcarin pack where host females had oviposited. *L. hesperus* females were allowed to oviposit in a Gelcarin pack for 24 h. The Parafilm, from the side of the Gelcarin pack with eggs, was removed using a razor blade. When the Parafilm was removed, most of the eggs that had been embedded in it were also removed. The Parafilm was replaced with a clean piece of Parafilm, and two punctures (1.0–1.6 mm in diameter) were made in the clean Parafilm with a clean pair of fine-pointed forceps. These holes simulated holes made by *L. hesperus*. Individual *A. iole* females were then placed on the Parafilm with two punctures. Their behavior was observed (for up to 5 min) and ovipositor probing was recorded. As a control, we used Gelcarin packs that had not been exposed to *L. hesperus* adults, one side of which had been replaced with a clean piece of Parafilm into which two punctures were made, as described above. For each treatment, we tested 10 females each day for 4 days.

To eliminate the possibility that a female's response might be due to the presence of Gelcarin, the following experiments were conducted. The depression of a medium thickness glass hanging drop microscope slide (Fisher Scientific, Cat. No. 12-560A) was filled with 0.15 ml of a test material and covered with a piece of Parafilm (25 × 25 mm), which was punctured with forceps as described above. Then, an individual *A. iole* female was placed on the punctured Parafilm covering a test material, and her behavior was observed until she inserted her ovipositor into the punctures twice or for up to 5 min. The test materials were distilled water, Rinaldini solution (Sigma, St. Louis, MO) as a physiological saline solution, host female contents, host male contents, or nothing.

The host male or female contents were obtained as follows. *L. hesperus* males or females were killed in 70% ethanol and immediately placed in 0.1 ml of distilled water on a glass slide. The anterior and posterior ends of the abdomen were held with forceps and pulled apart. The abdominal integument was broken and the abdominal contents were mixed with the distilled water. The contents (0.15 ml) were used for the experiments. For each treatment, we tested 7 females each day for 4 days.

Because we had observed that females often stopped antennating and preened their antennae after direct contact with test liquids, we observed female behavior on Parafilm on which the test materials were applied only to the punctures. A droplet (0.15 ml) of distilled water, host female contents, or host male contents was placed in the depression of a hanging drop microscope slide. The tips of a pair of forceps were dipped into the droplet of solution and then used to puncture the Parafilm. The punctured Parafilm was placed on a microscope slide, an individual female was placed on the Parafilm, and her response to the punctures was observed (for up to 5 min). For each treatment, we tested 7 females each day for 4 days.

Effect of Host Feeding Punctures on A. iole Females

L. hesperus probe Gelcarin packs with their mouthparts, apparently to obtain water, and leave salivary secretions on the surface of the Parafilm. Thus, to determine if *L. hesperus* salivary secretions induce ovipositor probing behavior in *A. iole* females, the following experiment was conducted. Gelcarin packs were exposed to *L. hesperus* nymphs for 1 day. Only water was supplied in the rearing cage. A piece of the exposed Parafilm (25 × 25 mm) was then removed from the Gelcarin pack that had been exposed to nymphs, and two punctures were made, with forceps, as described above. The piece of punctured Parafilm was placed on a glass hanging drop slide filled with distilled water. An individual *A. iole* female was placed on the punctured Parafilm and observed for ovipositor probing (for up to 5 min). As a control, the response of females to punctured Parafilm removed from a Gelcarin pack, that had not been exposed to *L. hesperus* nymphs, was observed. For each treatment, we tested 7 females for 3 or 4 days.

Kairomone Sources

To identify potential sources of the kairomone(s) stimulating ovipositor probing behavior in *A. iole* females, we observed responses to glass cylinders to which (1) hemolymph, (2) salivary gland, (3) seminal depository, (4) male content, or (5) female content materials had been applied. The materials were obtained as follows. To obtain *L. hesperus* female hemolymph, foreleg femurs were removed and squeezed with forceps to force a droplet of hemolymph from the opening. Salivary gland material was obtained by holding the prothorax and mesothorax of a *L. hesperus* female with forceps and gently pulling them apart on a glass hanging drop microscope slide. When the salivary glands appeared, they were carefully removed with forceps, placed in the depression of the slide, and rinsed three times with distilled water. Seminal depository material was obtained by dissecting the seminal depository of *L. hesperus* females, placing it in the depression of a hanging drop microscope slide, and rinsing it three times with distilled water. The contents of host males and females were obtained as described above. Each test material was placed in the depression of a hanging drop slide, and a glass cylinder (0.5–0.6 min in diameter) was dipped into the material. To mimic a host egg, the glass cylinder, covered with a test material, was then partially inserted into a puncture in a piece of Parafilm on a glass hanging drop microscope slide. The cylinder protruded 1.5–2.0 mm from Parafilm. We also observed the response of *A. iole* females to mature *L. hesperus* ovarian eggs. Ovarian eggs were dissected out of adult females and rinsed three times with distilled water. The eggs were embedded into punctures on a clean Gelcarin pack. Individual females were placed on a Gelcarin pack, and their behavior was observed for up to 5 min. Whether they probed the glass cylinders covered with a test material or ovarian eggs was recorded. For each treatment, we tested 7–10 females each day for 3 or 4 days.

The chi-χ^2 test and post hoc multiple comparisons in sample proportions for test of homogeneity were used to compare the proportion of female responses among treatments (Marascuilo and McSweeney, 1977).

RESULTS

Response of A. iole Females to Punctures in Gelcarin Packs with L. hesperus Eggs

A. iole females responded to punctures in clean punctured Parafilm on Gelcarin packs, which had contained *L. hesperus* eggs, in a manner similar to their response to host eggs (Conti, *et al.*, 1996). They intensively antennated the punctures, turned 180°, and antennated them again. After repeating these behaviors for 10–60 s, more than 70% of females probed, with their ovipositor, in or near the punctures in Parafilm for 10–70 s. However, less than half of females probed punctures in clean Parafilm on Gelcarin packs that had not been exposed to hosts. There was a significant difference in percentage of response to punctured Parafilm on packs that had contained eggs and punctured Parafilm on packs that had not contained host eggs ($\chi^2 = 5.2$, $df = 1$, $P = 0.02$) (Table 1), indicating the presence of an ovipositor probing stimulant for *A. iole* in Gelcarin packs that had been in contact with naturally deposited *L. hesperus* eggs.

Effect of Host-Derived Substances on Ovipositor Probing by A. iole Females

A. iole females did not probe punctures in Parafilm covering distilled water or nothing, in the depression of a hanging drop microscope slide, with their ovipositor (Table 2). Only 18% of the *A. iole* females probed punctured Parafilm covering liquid from clean Gelcarin packs. However, the majority (≥61%) of *A. iole* females

TABLE 1

Ovipositor Probing Response by *A. iole* Females to Gelcarin Packs, Which Contained Internal Liquid Derived from *L. hesperus* Adults or Eggs

Treatment	No. females examined	Percentage response[a]
Control[b]	40	47.5
Treatment[c]	40	72.5

[a] $\chi^2 = 5.21$, $df = 1$, $P = 0.02$.
[b] Clean Gelcarin packs whose surface Parafilm was replaced by clean punctured Parafilm.
[c] Gelcarin packs where *L. hesperus* adults had laid eggs and the surface Parafilm was replaced by clean punctured Parafilm.

did probe punctured Parafilm covering liquid from Gelcarin packs that had contained *L. hesperus* eggs, female contents or male contents. When females came into direct antennal contact with any of these liquids, they often stopped antennating and preened their antennae before resuming antennation.

When only the punctures in the Parafilm were coated with the contents of host males or females, more than 60% of the females probed the punctures with their ovipositor (Table 3). However, they did not probe punctures coated with distilled water.

Effect of Host Feeding on Ovipositor Probing by A. iole Females

When *A. iole* females were presented with punctured Parafilm removed from Gelcarin packs that had been exposed to host nymphs, they often antennated the substrate while walking in a zig zag pattern, and 24% of females used their ovipositor to probe the punctures (Table 4). Only 7% of females probed punctured Parafilm from plain Gelcarin packs, and unlike females on Parafilm that had been exposed to host nymphs, they walked in a straight line until they encountered the punctures in the Parafilm. The difference in percentage of response to punctured Parafilm exposed to host nymphs and clean Parafilm was not significant ($\chi^2 = 2.0$, $df = 1$, $P = 0.16$).

TABLE 2

Ovipositor Probing Response by *A. iole* Females to Punctured Parafilm Covering Test Materials in a Hanging Drop Microscope Slide

Treatment	No. females examined	Percentage response[a]
Nothing	28	0a
Distilled water	28	3.0a
Rinaldini solution	28	0a
Liquid from clean packs	28	17.9a
Liquid from packs with host eggs	28	70.4b
L. hesperus female contents	28	71.7b
L. hesperus male contents	28	60.7b

[a] $\chi^2 = 75.6$, $df = 6$, $P = 0.0001$. Percentages with different letters are significantly ($P < 0.05$) different by post hoc multiple comparisons in proportions for tests of homogeneity.

TABLE 3

Ovipositor Probing Response by *A. iole* Females to Punctures in Parafilm, Which Was Coated with Distilled Water, or *L. hesperus* Female or Male Contents

Treatment	No. females examined	Percentage response[a]
Distilled water	28	0a
Female contents	28	60.7b
Male contents	28	64.3b

[a] $\chi^2 = 30.1$, $df = 2$, $P = 0.0001$. Percentages with different letters are significantly ($P < 0.05$) different by post hoc multiple comparisons in proportions for tests of homogeneity.

Source of a Substance Inducing Ovipositor Probing in A. iole Females

When *A. iole* females were released near a glass cylinder coated with a test substance, most females did not orient to it, but walked in an approximately straight line until they came into contact with the glass cylinder. When they contacted a cylinder to which host hemolymph had been applied, they antennated the glass cylinder while walking on it for 20–140 s. Then, 98% of them probed the cylinder, or the substrate near it, with their ovipositor. Females also often probed glass cylinders that had been coated with seminal depository material, male contents, or female contents. However, they did not respond to glass cylinders coated with distilled water, and few females (19%) responded to cylinders coated with salivary gland material (Table 5). When ovarian eggs, which had been removed from host females and embedded into Parafilm, were contacted by *A. iole* females, they antennated and probed them, as they did to naturally embedded eggs (Table 5).

DISCUSSION

Previous studies suggested that chemicals derived from the substrate and from the host influence host location and recognition by *A. iole*, although the role of

TABLE 4

Ovipositor Probing Response by *A. iole* Females to Punctures in Parafilm Where *L. hesperus* Nymphs Probed with Mouthparts or to Clean Punctured Parafilm

Treatment	No. females examined	Percentage response[a]
Films with nymphs	21	23.8
Clean film	28	7.1

[a] $\chi^2 = 2.0$, $df = 1$, $P = 0.16$.

TABLE 5

Ovipositor Probing Response by *A. iole* Females to Glass Cylinders Coated with Materials from *L. hesperus* Adult Organs or to Mature Ovarian Eggs

Material	No. females examined	Percentage response[a]
Distilled water	28	0a
L. hesperus females contents	28	85.7b
L. hesperus male contents	28	92.9b
L. hesperus hemolymph	49	98.0b
L. hesperus salivary gland	21	19.0a
L. hesperus seminal depository	28	75.0b
L. hesperus ovarian eggs	28	89.3b

[a] $\chi^2 = 91.6$, $df = 6$, $P = 0.0001$. Percentages with different letters are significantly ($P < 0.05$) different by post hoc multiple comparisons in proportions for tests of homogeneity.

such chemicals was not proven (Conti *et al.*, 1996, 1997). Results of the present study strongly indicate that chemicals derived from hosts play an important role in host recognition and acceptance by this parasitoid. While parasitoid females did not probe punctured clean Parafilm or clean glass cylinders embedded in Parafilm with their ovipositor, they did probe the punctures or the glass cylinders when the internal contents, hemolymph, and seminal depository of *L. hesperus* females or internal contents of males were present.

The role of kairomones in host recognition and acceptance behavior of several egg parasitoids attacking exposed eggs has been studied (Nordlund *et al.*, 1987). All host recognition kairomones of egg parasitoids reported to date are produced in the reproductive system of the adult host female (Bin *et al.*, 1993). Accessory gland materials from adult host females stimulate ovipositor probing and drilling by parasitoids of lepidopteran eggs or cockroach ootheca (Schmidt, 1994; Nordlund *et al.*, 1987; Vinson and Piper, 1986). In *Trissolcus basalis* Wollaston, an egg parasitoid of the stink bug *Nezara viridula* (Linnaeus), host egg adhesive contains a host recognition kairomone, and the adhesive is produced by the follicular cells in the ovarioles of the host female (Bin *et al.*, 1993). In the present study, females responded to punctured Parafilm covering liquid from packs with host eggs, which indicates two possible kairomone sources. First, the chorion of host eggs might contain a kairomone, which dissolves in the liquid of the pack. Second, *L. hesperus* might secrete chemicals during oviposition into the pack. However, we could not identify the specific source of the host recognition kairomone though our results indicate that the kairomone is associated with the reproductive system of host females. The fact that *A. iole* females responded to mature ovarian eggs from host females suggests that the kairomone is present on the chorion of ovarian eggs. *A. iole* females responded strongly to the hemolymph of host females. The internal abdominal contents of both males and females induced an ovipositor probing response in *A. iole* females. These fluids consisted mainly of hemolymph because care was taken not to damage the internal organs. Thus, some substance common to both *L. hesperus* egg chorion and hemolymph contains the kairomone(s). It is unlikely that *L. hesperus* females release hemolymph during oviposition. Seminal depository materials also induced ovipositor probing in *A. iole* females. This may indicate that the organ is a potential source of the kairomone(s). But, again, the seminal depository may contain substances that also occur in hemolymph and egg chorion, which are involved in host recognition by *A. iole*. Further research is needed to identify the source of the kairomone(s).

Physical properties of the part of the eggs that protrudes from the plant surface are also important in host recognition and acceptance by *A. iole*. Conti *et al.* (1996) showed that *A. iole* females accepted partly embedded eggs more frequently than fully exposed eggs or fully embedded eggs. In the present study, most (98%) females responded to hemolymph-coated glass cylinders (0.5–0.6 mm in diameter), a part of which protruded 1.5–2.0 mm from Parafilm. But only four out of seven females probed hemolymph-coated glass cylinders of the same size when they were laying on Parafilm. None of eight females probed a larger hemolymph-coated glass cylinder (1.5 mm in diameter) protruding 2.0 mm from Parafilm, although they antennated it for 50–100 s (Takasu and Nordlund, unpublished).

Artificial punctures in Parafilm, coated with hemolymph or other host-derived substances, were often probed by females. Conti *et al.* (1996) observed similar probing of Gelcarin packs with artifical wounds. However, flat, unpunctured Parafilm coated with hemolymph did not induce a female probing response. These facts indicate that physical properties of the substrate, such as a concave surface, play a role in host recognition. When host hemolymph was applied to flat Parafilm and presented to *A. iole* females, they occasionally antennated the spot where hemolymph had been applied, but they never probed the Parafilm with their ovipositor.

Conti *et al.* (1996) suspected that plant exudates might play a role in host recognition by *A. iole*. Although host-derived chemicals and the physical properties of the glass cylinder triggered probing behavior of *A. iole* in the present study, our results also indicated that the physical presence of Gelcarin gel underneath Parafilm may be partly responsible for the probing response observed. Although females did not respond to punctured Parafilm covering distilled water or nothing, 47% of females responded to punctured Parafilm on plain Gelcarin packs. Because only 18% of females responded to punctured Parafilm covering liquid from the plain Gelcarin packs, the response to

punctured Gelcarin packs cannot be explained by the liquid alone. We observed that when there was no water or Gelcarin gel underneath tested Parafilm, females walked on the substrate without antennating until they contacted a glass cylinder or a puncture. Vibration-reflecting substrates are important factors in the host recognition process of parasitoids attacking cryptic hosts (Meyhöfer and Casas, 1999). The Gelcarin packs, which consist of Parafilm and Gelcarin, simulate plant structures: the former imitates the wax surface and the latter the plant tissues. When *A. iole* females antennate the substrate, and then perceive the presence of plant tissues or Gelcarin gel underneath the substrate possibly through vibration, they may probe to examine a potential host protruding from or a puncture in the substrate.

Although salivary gland substances from *L. hesperus* did not stimulate ovipositor probing behavior in *A. iole* females, it may be a factor stimulating antennation. When punctured Parafilm from a Gelcarin pack that had been fed on by *L. hesperus* nymphs was presented to female *A. iole*, they walked in a zig-zag pattern and more often antennated the substrate, whereas they walked in a straight line and rarely antennated the substrate from clean Gelcarin packs. The surface of the Parafilm that had been exposed to *L. hesperus* nymphs contained saliva, deposited during the feeding process, and *L. hesperus* saliva may be a good indicator of their presence. Thus, *A. iole* may use this as a short-range host-searching cue.

In summary, like other egg parasitoids attacking exposed hosts, *A. iole* females that attack host eggs partially embedded in plant tissues use both chemicals derived from host adults or eggs and physical properties of protruding part of eggs as host recognition and acceptance cues. In addition, physical and chemical properties of the substrate in which host eggs are embedded could be important for probing response by this parasitoid.

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